

Hawaiian Miridae (Hemiptera: Heteroptera): The Evolution of Bugs and Thought¹

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ABSTRACT: Composition of the Hawaiian Miridae is unusual in the preponderance of the subfamily Orthotylinae, with at least 10 independent colonizations. Most of these colonizations appear to have Indo-Pacific origins, but at least some taxa are derived from North and South America. Collections and research on Hawaiian Miridae began with Blackburn in the 1880s and Perkins from 1890 to 1910. They collected only the common and larger taxa. Specimens of smaller, more delicate species generally did not survive intact to reach museums, and there was little focus on host-plant associations. These two workers collected 85% of the known genera, but a relatively small number of species. Kirkaldy described the generic-level taxa from Blackburn's and Perkins' specimens in the early 1900s, but he failed to recognize the species-level diversity of the Hawaiian fauna. From 1905 to 1940, workers with the Hawaiian Sugar Planters' Association focused on host plants and collected most species of host-specific Miridae. In the 1960s and 1970s, Robert Usinger and Wayne Gagné associated some groups of Hawaiian Miridae with their host plants and began to publish descriptions of these patterns. In the 1980s and 1990s the first phylogenies were constructed and biogeographic and evolutionary hypotheses were proposed. Current information indicates a myriad of mirid evolutionary patterns in Hawai'i, including (1) nonhost specific and no island endemism, (2) nonhost specific single-island endemism, (3) radiations on related host plants, (4) radiations on unrelated host plants, (5) sympatric speciation within islands, and (6) allopatric speciation between islands, within islands between mountains, and within mountains.

MIRIDAE IS THE largest family of Heteroptera, with a described world fauna of almost 10,000 species (Schuh 1995). They are distributed worldwide and are apparently adept at dispersal, with endemic species, and usually at least small radiations, on virtually all tropical oceanic island groups. This is also the pattern in the Hawaiian Islands, where the Miridae are the most diverse and species-rich group of Heteroptera, yet also the most poorly understood. There appears to have been at least 15 independent colonizations, with new discoveries continuing. The number of endemic species is well over 100, with the upper limit unknown at this point (Nishida 1994).

In this paper I provide both an overview of plant bug evolution in Hawai'i (a biological perspective) and an overview of the evolution of our understanding of plant bugs in Hawai'i (the historical view).

Generic Composition and Origins

Four of the eight subfamilies of Miridae have native taxa in Hawai'i. The fauna is dominated by the subfamily Orthotylinae with 11 genera, 10 of which are endemic to Hawai'i. The other subfamilies have endemic Hawaiian species in nonendemic, widely distributed genera. The diversity of the Orthotylinae fauna is unusually high in Hawai'i, representing 73% of the Miridae genera in Hawai'i compared with 18% of the world fauna (Figure 1). This pattern in Hawai'i is significantly different ($\chi^2 = 218$, $P < 0.0001$) from that of the source world fauna and is not

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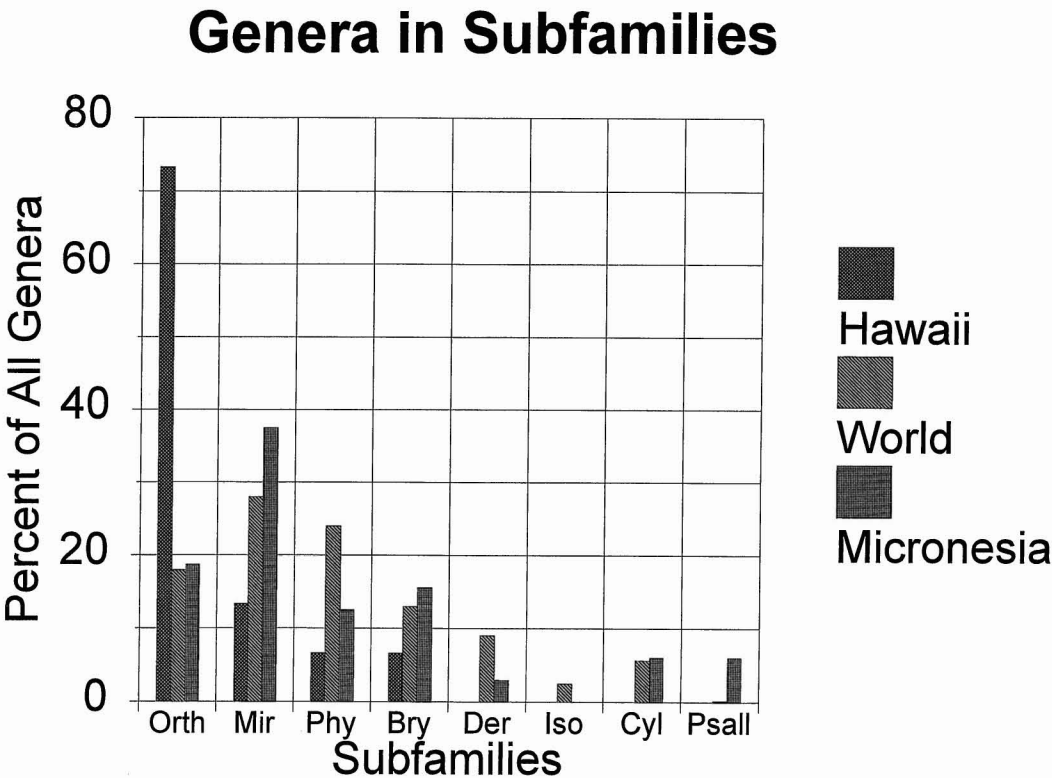


FIGURE 1. Distribution of genera among subfamilies of Miridae. Comparison of the Hawaiian, Micronesian, and world faunas. Orth, Orthotylinae; Mir, Mirinae; Phy, Phylinae; Bry, Bryocorinae; Der, Deraeocorinae; Iso, Isometopinae; Cyl, Cylapinae; Psall, Psalllopinae.

just typical of oceanic islands. As a comparison, the composition of the Micronesian mirid genera (Carvalho 1956) does not differ significantly from that of the world fauna. The preponderance of Orthotylinae in Hawai‘i is unlikely the result of greater dispersal capabilities. In fact other remote Pacific island groups such as Samoa and the Marquesas are depauperate of Orthotylinae, suggesting that they are actually poor dispersers compared with other subfamilies.

Zimmerman (1948a) was the first to speculate on the biogeographic origins of any of the Hawaiian Miridae and believed that they were all derived from Indo-Pacific taxa. This may be true for most of the groups; we now know that the genera *Opuna* Kirkaldy (Schuh 1984) and *Hyalopeplus* Stål (Carvalho and Gross 1979) are widespread Indo-Pacific taxa with endemic species in Hawai‘i, and the endemic genus *Kamehameha* Kirkaldy is probably derived from

the Indo-Pacific genus *Pseudoloxops* Kirkaldy (Asquith and Cassis in press). However, at least one genus, *Sarona* Kirkaldy, is almost certainly derived from a western North America taxon (Asquith 1994b). The genus *Koanoa* Kirkaldy may be derived from a Central American or South American *Ceratocapsus*-like ancestor (T. J. Henry, pers. comm., 1996). When other taxa are examined I suspect that the origins will prove to be diverse.

Understanding the Hawaiian Genera

Our understanding of the Hawaiian mirid genera came from the early entomological collections in Hawai‘i (Table 1). Kirkaldy (1902) first identified and described the Hawaiian mirid fauna at the generic level. Kirkaldy was unusual (Figure 2). Usinger (1942:4) tactfully described him as an “eminent, though somewhat unortho-

TABLE 1

A TIMELINE OF WORKERS WHO HAVE CONTRIBUTED TO
OUR UNDERSTANDING OF THE HAWAIIAN MIRIDAE

DATE	COLLECTORS
1850	During the Eugenies Resa Expedition in 1852, J. G. H. Kinberg collected Heteroptera, from which the first Hawaiian mirid, <i>Hyalopeplus pellucidus</i> Stål, was described.
1870	The Reverend Thomas Blackburn collected in the Islands from 1876 to 1882. Most of his material was sent to and described by Buchanan White, who did not work on the Miridae, so the material was not used at the time.
1890	R. C. L. Perkins made extensive collections in Hawai'i from 1892 to 1897, providing most of the material for the <i>Fauna Hawaiiensis</i> work.
1900	George W. Kirkaldy wrote the Miridae section for <i>Fauna Hawaiiensis</i> and worked in Hawai'i from 1903 to 1905.
1905–1925	O. H. Swezey, W. G. Giffard, and F. Muir were avid and competitive collectors with the Hawaiian Sugar Planters' Association. They collected Miridae along with their primary focus on Delphacidae and host plants.
1925–1950	Otto Swezey and F. X. Williams continued the collecting began by the earlier trio.
1935	Robert L. Usinger collected in Hawai'i in 1935 and made important host-plant associations.
1950–1990	John W. Beardsley focused mostly on Sternorhyncha, but also collected mirids and provided important host-plant information.
1968–1988	Wayne C. Gagné was the first worker to focus on the Hawaiian Miridae, revising the endemic genus <i>Nesio-miris</i> . He also made the most extensive and important collection of Miridae to date.
1990–present	A. Asquith has been focusing on the Miridae since 1990, revising the endemic genus <i>Sarona</i> .

NOTE: I do not mean to imply that these are the only people who have collected mirids in Hawai'i, but based upon museum collections and published works, these people have contributed substantially to our understanding of diversity and evolution.

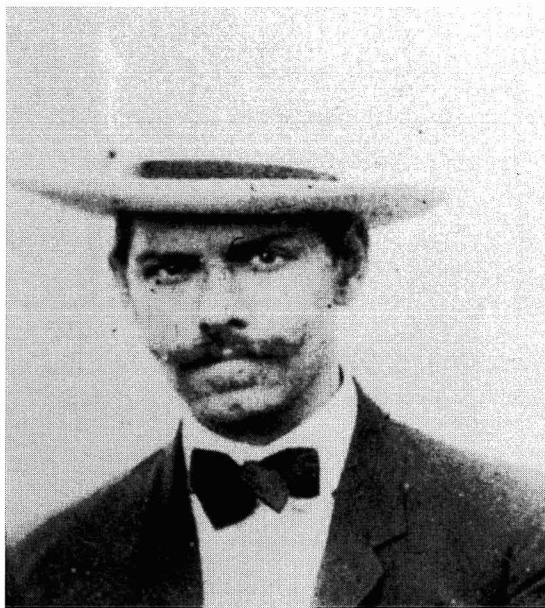


FIGURE 2. George W. Kirkaldy: Scottish hemipterist who described most of Hawai'i's endemic genera of Miridae.

dox Scotch Hemipterist" and noted that "everywhere in Hemiptera literature he left a touch of genius and almost complete chaos." This is true of his work on the Hawaiian Miridae. Kirkaldy addressed both the generic- and species-level evolution of the Hawaiian Miridae. He accurately described one, but completely missed the other.

Kirkaldy recognized the distinctness of the endemic Hawaiian genera by erecting new tribes for *Sulamita* Kirkaldy, *Kalanina* Kirkaldy, and *Pseudoclerada* Kirkaldy. Although these tribes are no longer recognized (Schuh 1974, 1995), all but one of Kirkaldy's nine endemic Hawaiian genera are still valid and probably will continue to be. Most of Kirkaldy's genera of Hawaiian Miridae were based upon Blackburn's and Perkins' collections. Two additional endemic genera of Hawaiian Miridae were collected and recognized in the 1980s and 1990s, both unusual taxa restricted to *Pritchardia* Seem. & H. A. Wendl. palms (Asquith 1994a, unpubl. data). Additional work on the Hawaiian genera will probably focus on phylogenetic positions and distinctness. For example, the genus *Opuna*, originally thought to be a Hawaiian endemic (Kirkaldy 1902), was synonymized with the cos-

mopolitan genus *Campylomma* Reuter (Zimmerman 1948b) and is now recognized as a widespread Indo-Pacific taxon (Schuh 1984).

Historical Understanding of Hawaiian Species Diversity

Blackburn and Perkins collected numerous Heteroptera during their work in Hawai‘i, and Usinger (1942) noted that “Perkins’ extensive field work turned up most of the species of *Nysius* known today.” Even compared with our current understanding of the fauna, these two workers collected over 50% of the species in this genus of Lygaeidae (Figure 3). This is strongly contrasted by the Miridae, where Perkins and Blackburn did not really scratch the surface. In *Sarona*, for example, they collected less than 20% of the species currently known (Figure 3).

This very incomplete sample shaped Kirkal-

dy’s concept of the species-level evolution of the Hawaiian plant bugs. He did not believe that genitalic structures were of any evolutionary significance. Likewise, he treated size and color differences among most taxa as intraspecific variation. Comparing his study of the Miridae with studies of the species of *Plagithmysus* Motschulsky, *Oodemus* Boheman, *Proterhinus* Sharp, and *Hylaeus* Fabricius, he wrote “I can only say that after the most exhaustive study, I cannot achieve anything like these results. Whether it be due to a constitution in the Rhynchota differing from that of the other orders I cannot say; I can only see a large assemblage of forms varying in the most bewildering fashion, forming incipient species, if one will, but at the same time forming links of such a character that it seems unreasonable to attempt arbitrary definition of many ‘species’ ” (Kirkaldy 1902:42). Therefore, Kirkaldy described multi-

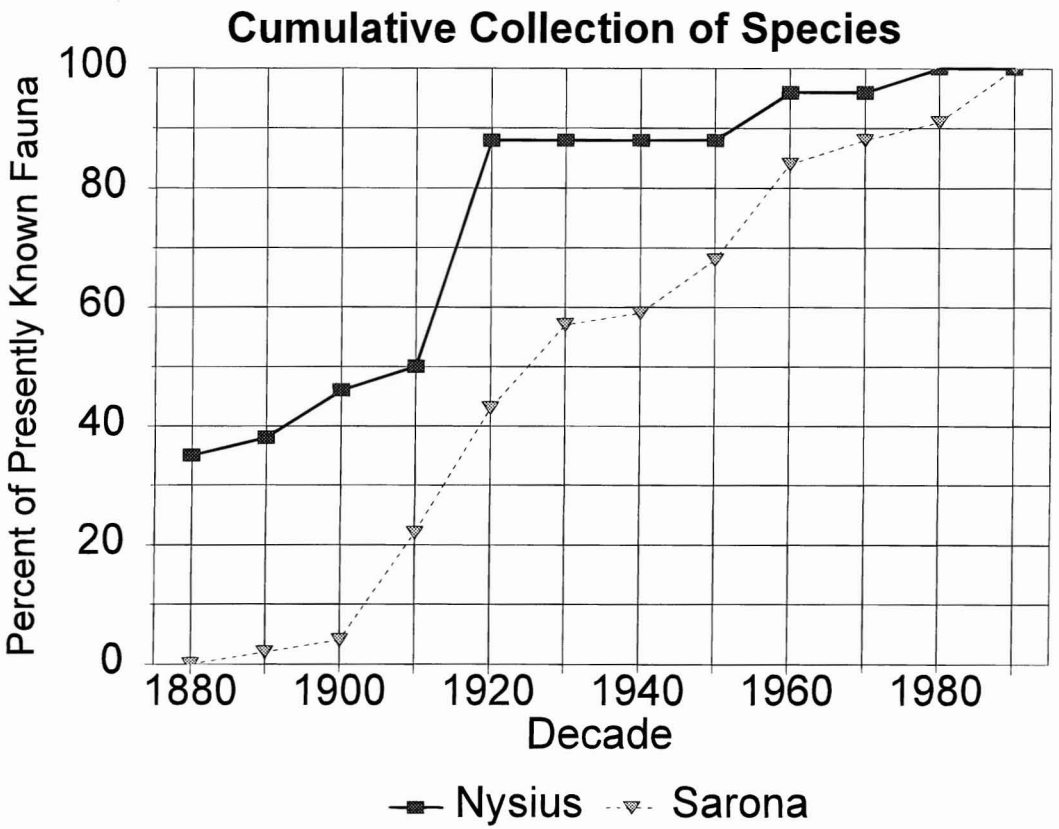


FIGURE 3. Cumulative collection of Hawaiian *Nysius* species (Lygaeidae) and *Sarona* species (Miridae) through time.

ple species in only four of the 12 speciose genera. At least in part, Kirkaldy's dismissal of the species-level evolution of the group may have been due to the lack of sufficient material. At the time of the first *Fauna Hawaiiensis* work, he had not been to Hawai'i and was relying largely on Perkins' collections. Most Miridae are extremely fragile and Perkins did not focus on this group, so that in the speciose and abundant genus *Orthotylus* Fieber, for example, Kirkaldy had only about 100 specimens to examine. However, as early as 1888, Blackburn described the plant bugs in Hawai'i as "rather plentiful" and indicated that he had representatives of almost 40 species. Even Perkins recognized that there was more diversity than what Kirkaldy had indicated, and he described three additional species in 1912.

Our understanding of species diversity began in 1905 when Walter Giffard of the Hawaiian Sugar Planters' Association (HSPA) hired several entomologists to work on biological control of the sugarcane leafhopper, including Otto Swezey, Frederick Muir, and later R. C. L. Perkins and F. X. Williams. The HSPA group of Swezey, Muir, Giffard, and Williams were avid and competitive collectors (Figure 4). Most of them focused mainly on the Homoptera, but they also collected Miridae. Because most of the Homoptera are also host-plant specific, they recorded hosts and thus also made important plant associations for the Miridae.

Although Robert L. Usinger only spent about a full year in Hawai'i, he was an ardent collector. Not only did Usinger collect a great deal of material, he also spent time in the field with Ray Fosberg, an eminent Pacific botanist, and learned the Hawaiian flora. He also spent time with Otto Swezey and was probably strongly influenced by him or at least greatly benefitted from discussions with him (Usinger 1972). For many years Swezey had collected Homoptera from every conceivable host plant, and by the time Usinger arrived, Swezey was working on host-plant associations of Hawaiian Lepidoptera. Therefore, probably in no small part because of Swezey, the first work to recognize the host-plant associations of any Hawaiian Heteroptera was Usinger's 1942 study of the orsiline Lygaeidae. In that work he concluded that

"The geographical distribution of phytophagous insects is so closely related to their plant hosts that the two can scarcely be dealt with separately" (1942:135).

In the 1960s, the Hawaiian fauna of the plant bug genus *Cyrtopeltis* Fieber was revised by José Carvalho and Usinger (1960), and later by Usinger's student Wayne Gagné (1968). These were the first works to associate Hawaiian plant bugs with specific host plants, and they set the stage for all later work. Even with the recognition of the host association in this genus, the rare occurrence of *Cyrtopeltis* on rare and unrelated plants has led to a driplike rate of understanding of this group. Even after two revisions, Gagné discovered three new species in the 1970s and 1980s (unpubl. data), and an additional one was found in 1990 (Asquith 1993). In 1992, while examining an herbarium specimen of a newly discovered species of *Cyrtandra* J. R. Forster & G. Forster from Kaua'i, I found a crushed *Cyrtopeltis* nymph that undoubtedly represents a new species. The work on *Cyrtopeltis* underscores the need for additional collecting and host-plant sampling.

Not until Gagné began his work on *Nesiomiris* Kirkaldy did the truly remarkable diversity and evolution of the Hawaiian plant bugs begin to come to light. Beginning with a monotypic genus, he found 50 new species, each strictly host specific or feeding on a few closely related hosts (Gagné 1965). Most species of *Nesiomiris* feed on Araliaceae, including *Cheirodendron* Nutt. ex Seem., *Tetraplasandra* A. Gray, and *Munroidendron* Sherff. It is presumed but not demonstrated that Araliaceae is the plesiomorphic host association. The reasoning is that only one clade has switched to feeding on *Ilex* L. No members of the *Ilex* clade occur on Kaua'i. In fact plesiomorphic members of the *Ilex*-feeding clade occur on Maui Nui and derived taxa on O'ahu; thus it appears that the switch to *Ilex* was recent and occurred on Maui Nui. There are clear examples of host-associated speciation events in *Nesiomiris*, where sympatric sister taxa inhabit different species of *Cheirodendron*.

But most speciation in *Nesiomiris* appears to have been allopatric, and analysis of sister-taxon distributions shows areas of endemism. This is particularly true of the *Ilex*-feeding clade on



FIGURE 4. Hawaiian Sugar Planters' Association workers Otto Swezey, Frederick Muir, C. E. Pemberton, and F. X. Williams at the summit of Mount Ka'ala, 1925.

O'ahu, with species endemic to the Mount Ka'ala summit forest, the northern Wai'anaes, the southern Wai'anaes, and Pu'u Manamana (the range above Ka'a'awa). It is interesting that the northern Ko'olaus have a different species than the southern Ko'olaus, but they are not sister taxa, and each also occurs in part of the Wai'anae Range (Figure 5). And although most speciation of *Nesiomiris* on Kaua'i was apparently sympatric and host-plant mediated, there are two examples of allopatric sister taxa on the same host, which identify the Makaleha Mountains as an area of endemism on Kaua'i (Figure 6).

Similar to Gagné's finding with *Nesiomiris*, my work on another presumed monotypic genus, *Sarona*, also found 40+ new species (Asquith 1994b). With only one exception, all species of *Sarona* are single-island endemics, and all are also strictly host specific, never feeding on more than one host-plant species. Unlike *Nesiomiris*, which has made relatively few host-plant switches, however, species of *Sarona* feed on 17 genera of plants in 14 different families, from

the large, common forest tree *Metrosideros polymorpha* Gaud., to the small, parasitic *Korthalsella complanata* (Tiegh.) Engl. (Asquith 1994b). Thus most speciation events in *Sarona* appear to have been sympatric and host mediated (Asquith 1995). For example, all Kaua'i species, except *S. mokiha*, are monophyletic. Most species, including *S. mokiha*, are largely sympatric and feed on different species of *Melicope* J. R. Forster & G. Forster, sometimes with branches intertwined. I interpret this as an example of radiation on related hosts. By contrast, the Big Island clade (Asquith 1995) is an example of host-mediated radiation but on unrelated hosts. Members of this clade occur on plants in at least five different families. Although there are examples of interisland allopatric speciation in *Sarona*, the general pattern of evolution in this group is host-mediated sympatric speciation, on related or unrelated hosts.

In contrast to the patterns observed in these genera, I here examine data on three less-speciose groups of Hawaiian plant bugs, the genera *Hyalopeplus*, *Kamehameha*, and *Pseudoclerada*.

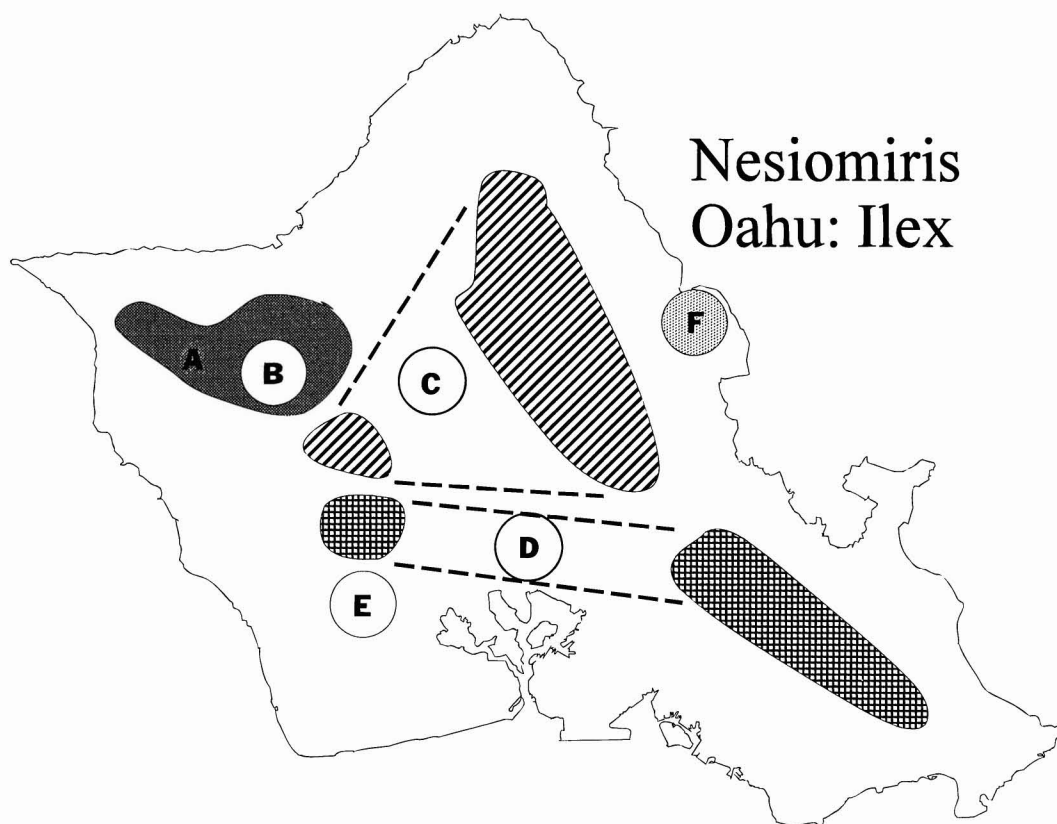


FIGURE 5. Distribution of *Ilex*-feeding species of *Nesiomiris* species on O'ahu (adapted from Gagné [1965]).

Hyalopeplus Kirkaldy

Hyalopeplus pellucidus Kirkaldy, a phytophagous but not host-specific species, occurs on all the main Hawaiian Islands. It is an endemic species, but belongs to a genus that is widespread in the Pacific, with species in Fiji, Samoa, and the Marquesas. This is an example of a colonization in which there has been little differentiation from ancestral taxa, and it has not radiated ecologically nor differentiated by island. Because of its similarity to other species and broad host range, *H. pellucidus* was long considered to be an introduced species in Hawai'i (Zimmerman 1948b). It was not until the entire genus *Hyalopeplus* was revised by Carvalho and Gross (1979) that *H. pellucidus* was recognized as a Hawaiian endemic. This example demonstrates the need for understanding the taxonomy and systematics of the group outside of Hawai'i so

that patterns within Hawai'i can be properly interpreted.

Kamehameha Kirkaldy

Kamehameha is an endemic Hawaiian genus that is likely derived from an Indo-Pacific group of *Pseudoloxops* (Asquith and Cassis in press). Species are nocturnal predators and are not specific to any host plant. They are most frequently encountered in higher-elevation mesic to wet forest habitats, but I have also taken them from dry forest in leeward gulches on O'ahu.

There are only three species of *Kamehameha*, one endemic to the remote northwestern island of Nihoa, one endemic to Kaua'i, and one species occurring on all the rest of the Islands from O'ahu to Hawai'i (Figure 7). Thus, *Kamehameha* has not speciated by island except on those

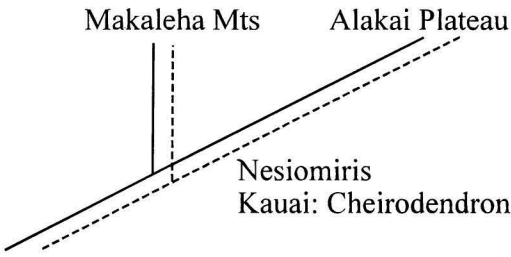


FIGURE 6. Distribution and relationships of four species of *Cheirodendron*-feeding *Nesiomiris* on Kaua'i, showing the Makaleha Mountains as an area of endemism.

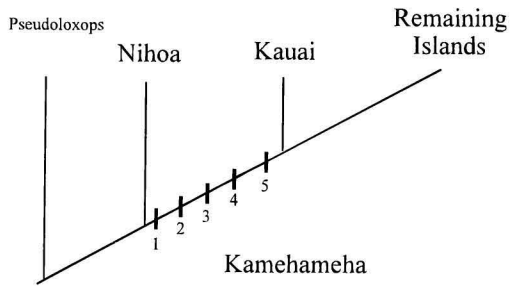


FIGURE 7. Distribution and relationship of species of the endemic Hawaiian genus *Kamehameha*. Characters are discussed in the text.

two that are separated from others by more than 100 km. Likewise, there appears to have been little or no change in the ecologies of these species, at least not on Kaua'i and the other main Islands. Little is known about the species on Nihoa. It has only been collected once, from *Pritchardia* palms in the only moist gulch on the island. Likely, all these species once inhabited mesic canopied forest down to sea level.

The distribution of *Kamehameha* species may represent a typical example of allopatric speciation by dispersal from older to younger islands. In this hypothesis, *Kamehameha nihoa* Asquith is the oldest, most plesiomorphic taxon, with *Kamehameha kaumualiii* Asquith and *K. lunailo* Kirkaldy being derived sister taxa (Figure 7). Using Micronesian *Pseudoloxops* taxa as an outgroup, there are at least five characters that support this hypothesis: (1) greatly elongate hemelytra in males, (2) greatly elongate second antennal segment, (3) metafemur mostly dark, with light spots, (4) scutellum strongly tumid, and (5) longitudinal sulcus on vertex very deep.

I am cautious in my support of this hypothe-

sis, however, because the Nihoa taxon inhabits a very different environment and its character states may represent autapomorphic losses or reversals. Nonetheless, *Kamehameha* is important because it is the only example among the Hawaiian Miridae of basal and presumably relictual taxa on the northwestern islands. Because *Kamehameha* is not host-plant or even very habitat specific, it is not entirely surprising that this taxon has persisted in the limited habitat left on Nihoa. It lends support to the hypothesis that taxa from other genera also occurred on Nihoa and the other northwestern islands when upland habitats were available.

Apparently neither Blackburn nor Perkins obtained specimens of *Kamehameha* from Kaua'i, or at least Kirkaldy (1902) did not see any for his description of *Kamehameha lunailo*. It is surprising that the HSPA collecting group, including Swezey, did not obtain specimens of *Kamehameha* from Kaua'i. It was not until the 1960s that representatives of this genus were found on Kaua'i. This is partly because Swezey and the other HSPA entomologists spent considerably less time on Kaua'i and, based on my own experience, partly because the island endemic *K. kaumualiii* is much less common than *K. lunailo* on the other Islands.

Pseudoclerada Kirkaldy

Pseudoclerada is an endemic Hawaiian genus with unusual coleopteroid facies. Species are not host-plant specific and appear to be predaceous. They are inhabitants of mid-elevation wet gulches and mid- to high-elevation mesic to wet forests. Most species are taken as individuals and usually from moss-covered branches. At least some species appear to be nocturnal, and Perkins (1913) reported them under bark and in the leaf axils of *Freycinetia arborea* Gaud. Kirkaldy (1902) had specimens of *Pseudoclerada* from all the Islands collected by Perkins, but because he was not discriminating, he initially recognized only a single species, *P. morai* Kirkaldy. Later (Kirkaldy 1908) he described an additional species from the Big Island. Zimmerman (1948b) noted that there were obviously more species than what Kirkaldy recognized and that there was at least one species endemic to each of the Islands.

In reviewing *Pseudoclerada*, I have found at least 18 species, most of which are single-island endemics. Provisionally, I recognize four groups of *Pseudoclerada*: The "poopuu group" has taxa on all the main Islands, typically with island-endemic species, except for East Maui, West Maui, and Hawai'i, which all share a single species. This latter species and the Moloka'i species are clearly sister taxa and both have brachypterous females. The "moikeha group" also has taxa from Kaua'i to the Big Island, but no species are currently known from O'ahu or Lāna'i. Species in this group are extremely rare, however, and the absence of taxa on O'ahu and Lāna'i may be sampling error. The "eleele group" has taxa on O'ahu, Moloka'i, East Maui, and West Maui. Members of this group are also rare, and it is doubtful that this is the true distribution of the group. The "poopokele group" has only two species, one on Kaua'i and one on O'ahu. These species are the most commonly collected *Pseudoclerada*, and this Kaua'i-O'ahu distribution pattern probably reflects their true distribution.

It is hypothesized that there has been an older to younger island pattern of geographic allopatric speciation in all four groups of *Pseudoclerada*. At this point, because of the lack of discriminating morphological characters, only the "poopuu group" has been amenable to analysis, and this hypothesis is supported by only a few characters (Figure 8). But the only obvious deviation from this pattern is in the "eleele group," in which there are two species from the

Wai'anae range on O'ahu. There is little obvious pattern of ecological segregation among groups. On Kaua'i and O'ahu, the "poopokele group" may primarily inhabit mesic forest, whereas the "poopuu group" occurs in wet forest. Members of the "eleele group" and the "moikeha group" have been taken in dry, mesic, and wet forest habitats.

It is likely that we still do not have an adequate understanding of *Pseudoclerada* in Hawai'i. Perkins collected representatives of the "poopuu group" and the "poopokele group" on all the Islands. E. H. Bryan obtained a single specimen of the "eleele group" in 1920, and none was taken again until the 1960s. Likewise, no specimens in the "moikeha group" were collected before 1965. Thus, additional collecting will likely reveal other species on Islands for which we presently do not have group representatives. In addition, stronger phylogenetic hypotheses for *Pseudoclerada* are needed, particularly for relationships among groups, but will probably require nonmorphological data.

Conclusion

If the hypotheses of relationships and evolution within *Kamehameha* and *Pseudoclerada* hold with further analyses, then these are patterns in addition to those seen in other groups of Hawaiian Miridae. Thus, we have evidence for host-mediated sympatric speciation, host-mediated allopatric speciation between and within islands, nonhost allopatric speciation between and within islands, older to younger island colonization, younger to older island colonizations, and little or no differentiation within endemic taxa. As I have argued elsewhere (Asquith 1995), each group has its own history and unique course of evolution. The search for common patterns of evolution in Hawaiian Miridae has revealed only a diversity of patterns that is equal to the number of groups examined. Describing these patterns in their entirety, however, will require much additional collecting, with particular attention to host plants and to areas of endemism on all the islands that compose Hawai'i.

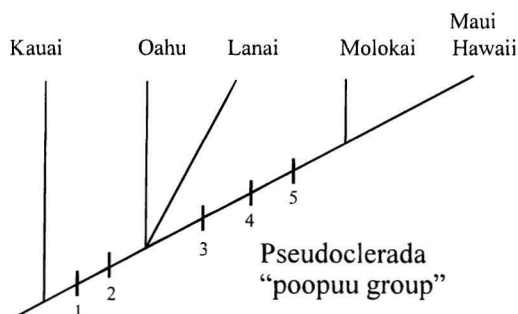


FIGURE 8. Distribution and relationship of species of the "poopuu group" of *Pseudoclerada*. Character states used in the phylogeny of this group: 1, basal half of hind femur black; 2, calli not tumid; 3, second antennal segment of male with long, erect setae; 4, female brachypterous; 5, tibiae banded.

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